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Title:

Evidence for long term change in length, weight and migration phenology of anadromous spawners in French Atlantic salmon *Salmo salar*

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Running headline:

Changing salmon size and phenology in France

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Abstract

We provide new data on Atlantic salmon *Salmo salar* life history traits across France, using a recreational angling database coming from fed by a mandatory catch declaration scheme over a large temporal (1987-2013) and spatial (n = 34 rivers) scale including three regions (genetic units). We reported new insights on changes in *S. salar* life history traits, with a decline in individual length, weight and a delay in the migration phenology of adult *S. salar* returning to French rivers. Similarities in time trends between regions may be attributable to common changes in environmental conditions at sea. Results also revealed different rates of change between early maturing fish (1SW fish) and late maturing fish (2SW fish), phenotypic traits being less variable and less impacted by environmental variations in freshwater returning 2SW fish than in 1SW ones. This study highlights the necessity to account for the variability in life history strategies when exploring mechanisms of phenotypic change in *S. salar*. Detailed data on *S. salar* in France have long been missing from the literature. This large scale study on French populations contributes to reduce the gap in knowledge by providing further empirical evidence of a global pattern in *S. salar* life history shared by all populations across the Atlantic Ocean, which is consistent with the widespread hypothesis of global response of populations to a major ecological mechanism during the marine phase of the life cycle.

Keywords

body size, environmental buffering, environmental variability, life history strategy, *Salmo salar*

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Introduction

Global climate warming in the Atlantic Ocean is responsible for rising sea surface temperature since the 1970's (Levitus et al., 2000; Polyakov et al., 2009). There is also strong evidence that climate change is altering ecosystem functioning, which is driving a major shift, observable across multiple trophic levels, in the North Atlantic (Durant *et al.*, 2004; Beaugrand *et al.*, 2008). Concomitantly, Atlantic salmon *Salmo salar* L. 1758 populations have suffered a tremendous decline in abundance across their distribution range (Jonsson & Jonsson, 2004; Chaput, 2012; ICES, 2016), together with marked changes in life history traits and population structure. In particular, a decline in the proportion of late maturing fish has been reported for many European and North American stocks (Baglinière *et al.*, 2004; ICES, 2016; Jonsson et al. 2016; Otero et al. 2012). Those changes have been accompanied by declines in age-specific length and weight of fish (Aprahamian *et al.*, 2008; Bacon *et al.*, 2009; Jonsson et al. 2016), together with a delay in adult migration timing (Todd *et al.*, 2012; Valiente *et al.*, 2011). Such changes are expected to affect population growth rate, raising concerns about the viability of this species of great patrimonial and economical value.

Identifying the causal link between latent driving factors and those phenotypic changes is difficult and may consist in one of the greatest challenges for fisheries ecology, and for *S. salar* in particular (Crozier & Hutchings, 2014). Due to a complex life cycle shared between freshwater and the marine environment, diadromous fishes are vulnerable to various factors of stress in a hierarchy of spatial scales (Armstrong *et al.*, 1998; Mather *et al.*, 1998; Lindburg & Waldman, 2009). Evidence now accumulates for a major impact of changes in the marine

environment encountered by *S. salar* (Jonsson & Jonsson, 2004; ICES, 2016; Jonsson *et al*., 2016). Both direct and indirect effects of rising sea surface temperature have been proposed. Temperature increase would impede post-smolt growth (Friedland *et al.*, 2000, 2005). In addition, temperature increase would decrease the productivity of North Atlantic pelagic food web, thus indirectly affecting feeding opportunities for salmon at sea (Friedland *et al.*, 2000; Peyronnet *et al.*, 2007; McCarthy *et al.*, 2008; Jensen *et al.*, 2011). In particular, the abundance and/or energy content of key pelagic crustaceans and small pelagic fish, on which *S. salar* largely prey, may have declined (Beaugrand & Reid, 2012; Friedland *et al.*, 2013; Mills *et al.*, 2013; Miller *et al.*, 2014). Recent stock rebuilding in some pelagic fish competing for similar resource as *S. salar* may further amplify this process (Jonsson et al. 2016; Mäntyniemi et al., 2012).

Simultaneous temporal trends in growth, length, weight and/or phenology variations have been observed in Norway (Jensen at al., 2011), Ireland (Quinn et al., 2006), and Scotland (Summers, 1995; Todd et al., 2008; Bacon et al., 2011). Given that those populations breed in very distant rivers, the existence of a large-scale mechanism taking at sea has been suggested. To go further, large scale data for Southern populations is required to confirm the influence and the extent of such global change. Yet, precise ecological and demographic mechanisms that underline those changes are still not clear (Crozier and Hutchings, 2014). Despite elusive causes, there is a need to better understand the factors regulating *S. salar* response to ongoing environmental change, for management and policy purposes.

In *S. salar*, anadromous adults mature after one winter at sea (1SW) or more than one winter at sea (MSW, i.e. up to five years) (Hutchings & Jones, 1998; Aas *et al.*, 2011). The differences in their respective life history traits (e.g. body size, growth rate, age at maturity, fecundity or migration timing) reflect the strategy of resource allocation to growth, survival and reproduction (Cody, 1966; Williams, 1966; Schaffer, 1983; Stearns, 1976). Under this strategy, alternative tactics seem to be partially determined by sex and genes (Fleming, 1996; Barson et al., 2015). Females, whose breeding success is strongly related to body size (Fleming, 1996), are more abundant among MSW, while males tend to mature earlier i.e. most of them are 1SW (Hutchings & Jones, 1998; Aas *et al.*, 2011). Thus, any change in resource availability or more generally in environmental conditions at sea is likely to induce contrasted response in 1SW and MSW, because of difference in their resource allocation (Stearns, 1976; Gaillard et al., 1989; Reznick et al., 1996). In Southern Europe, growing areas at sea used by MSW are farther away than in 1SW, resulting in an even greater contrast in mortality during sea migration between tactics. For instance, somatic growth might be more impacted by poor environmental condition at sea in 1SW, as energy allocation might be primarily dedicated to maturation in this group. Also, differences in age and sex-ratio between sea-age classes may confer different ability in buffering external forcing in 1SW and MSW, as already observed in mammals for instance (Coulson *et al.*, 2001). Monitoring life history traits by sea age class is essential to better understand and predict species response to ongoing global changes and provide sound insights for the management of *S. salar* across its distribution range (Armstrong *et al.*, 1998; Mather *et al.*, 1998).

In this study we investigated the long term change in length, weight and migration phenology of French *S. salar* populations over the last three decades, using a recreational angling

database coming from fed by a mandatory catch declaration scheme over a large spatial (n = 34 rivers) scale. Although the available literature accumulates evidence of temporal changes in life history traits in a high number of *S. salar* populations, only few results concern Southern Europe rivers (Valiente et al., 2011) and no results have been published for France so far. Extending the geographical range for which evidence of changes are documented is a prerequisite to test for the hypothesis of a common response of *S. salar* to environmental conditions at sea, and then refine our understanding of the factors driving those reported changes. We described how *S. salar* length, weight, body condition factor and annual migration timing have changed over the period 1987-2013 in French rivers. We investigated whether common patterns could be detected in geographically distant populations. We then tested the hypothesis of a tactic-dependent response to environmental variation in *S. salar*. Finally, we assessed the difference in individual response in 1SW and MSW, by analyzing the relative rate of change in key life history traits between 1SW and MSW over the study period. Overall, results brought new contributions to the understanding of the demographic and evolutionary forces that control *S. salar* response to environmental change in the Southern part of the species distribution range.

MATERIALS & METHODS

Recreational fishery data

Analyses are based on the French recreational angling database fed by a mandatory catch declaration scheme over a large temporal (1987-2013) and spatial (n = 34 rivers) scale. In France, *S. salar* recreational rod and line fishery takes place in more than 40 rivers of the Atlantic and Channel coasts, which are characterized by uneven spatial distribution and river profiles. These rivers are mainly localized in three regions that represent more than 90% of French *S. salar* abundance: Normandy, Brittany and Aquitaine (Fig. 1). This regional stratification results from previous analyses of both the genetic structure of French *S. salar* populations and based on their demographic and morphometric characteristics (Prévost, 1987; Perrier *et al.*, 2011). In addition to recreational fishery, a small commercial fishery takes place in the Adour River, Aquitaine region (on average 10.5 % of the annual salmon catches). The fishing season extends from the beginning of March to the end of October for rod fishing and to the end of July for commercial fishing. Since 1987, *S. salar* fishery rely on a national compulsory catch declaration scheme which offers a national sampling survey of adult *S. salar* and feed one of the largest dataset for salmonid fishery in Europe. Catch data are collected by anglers and centralized by the National Center for the Interpretation of Salmonid Catches. For each fish caught, the recorded data are date (D, day of the year), river, size (L, total length in mm), weight (W, in g) and a sample of scales. All scales are analyzed following a standardized protocol (Baglinière *et al.*, 1985) to estimate both the time spent in freshwater during the juvenile phase (freshwater age) and the time spent at sea during the adult phase of the life cycle, i.e. (sea-age). Current French populations are mainly composed of one sea winter (1SW), two sea winters (2SW) and rarely three sea winters (3SW) salmon. However, because of the unbalanced fishing effort between sea-age classes (being historically more intense on large 2SW fish than on 1SW ones), the data do not allow us to draw any inference on the relative abundance of the two tactics and its variation over time.

The ordinal date of capture (D) was considered as an index for the date of river entry. Indeed, as already discussed in Bacon et al. (2009), the rod capture data mostly concerns newly arrived fresh-run fish, often caught in lower parts of rivers just after their entry in freshwater. Several studies have shown that the movements and capture rates of *S. salar* decline rapidly after river entry (e.g., Thorley et al., 2005), suggesting that *S. salar* may be harder to catch by rod after several days in freshwater.

Because salmonids are considered to have a standard body shape, we used the condition coefficient of Fulton (K) as a proxy for *S. salar* body condition. It is calculated for each fish as $K= W/L^3$ (Bolger & Connolly, 1989; Nash *et al.*, 2006).

Quality control and data processing

Fish spending three winters at sea became scarce in French populations while repeat spawners are very rare (Baglinière & Porcher, 1994). Data from those fish were too few to allow reliable statistical analysis. They were thus removed from the study. Unrealistic combination of length and weight (i.e., K outside the range [0.4, 1.6]) coming from erroneous records, were discarded. The date of capture was also used as a filter criterion on the dataset. In France, *S. salar* migration is depending on sea age and hydrological conditions, with a MSW early run and a 1SW summer run (Baglinière & Porcher, 1994). Some years, late records are observed in the dataset, which correspond to a late upstream migration from the estuary as no

late run of "silver fish" are recorded on index rivers with fish trap facilities in France (e.g. Scorff River, E. Prévost, pers. com.). Also, the recorded length and weight of fish caught late in the season may be a biased proxy of the phenotypic traits of those fish at the time of their return. Indeed, fish caught late in the season often stayed several weeks in river waiting for favorable river discharge conditions to migrate upstream to spawning grounds. During this waiting period, fish may lose weight and the length of males may start to increase with the development of secondary sexual characters, such as the elongation of the upper jaw in the male salmon (Maisse & Baglinière, 1986; Baglinière & Porcher, 1994). Because sexual dimorphism is large enough to allow sex determination in salmon from September, we decided to only consider fish caught until the end of August for our analysis. Furthermore, fishery management could interfere with fish sampling, with late running fish being more likely to be under-represented in the dataset. Indeed, since 1994, *S. salar* recreational fishery in French rivers closes to preserve the targeted stock of spawners as soon as the allocated river-specific quota is reached (catch release is not implemented in France; Porcher & Prévost (1996)). Fishing closure often took place early in the season, leading to an uneven sampling of fish in fall.

In total, our analysis included 27,709 individual records (11,466 1SW fish and 16,243 2SW fish) collected over the period 1987-2013 on 34 rivers. Sample size per river was too small, thus records from single rivers were pooled into three study regions (Normandy, Brittany, and Aquitaine) to reduce sampling noise (Table I, Fig. 1). Despite an unbalanced number of river per regions and contrasted river profiles, this regionalization of the catch data reflects the spatial distribution of *S. salar* abundance in France. Populations from the Loire River and from Northern France, which represent less than 5% of the records, were excluded from the

dataset for three main reasons: i) salmon fishing in the Loire River has been forbidden since 1994; ii) salmon catches in Northern France are low; iii) stocking practice takes place on all these rivers, which may mask ecological signals (Le Cam *et al.*, 2015).

Statistical analyses

Characterizing temporal trends and the impact of covariates

Temporal trends in D, L, W and K (see Supporting Information A1 and A2) were analyzed using Generalized Additive Models (GAM) as implemented in the R package mgcv, V. 1.8-6 (Wood, 2011) to capture the non-linearity in the data. Independent models were built for each of the four response variables, here denoted Z for genericity. The effects of the sea-age class (1SW or 2SW), and regions (Normandy, Brittany, Aquitaine) were introduced as categorical effects, and the Year was considered as a continuous variable in the non-parametric smooth trend. The most complex model considered was:

$$Z_{Y,A,R,i} \sim A \times R + s(Y, A \times R) + \varepsilon_i,$$

where $Z_{Y,A,R,i}$ is the variable D, L, W or K for any fish *i* of sea-age A, caught at year Y in region R, 'A×R' is a sea-age by region interaction, s(Y, A×R) is a sea-age by region specific smooth time trend, and ε_i are independent and identically distributed residuals ~ $N(0,\sigma^2)$ for any individual fish *i*. To test for the existence of trends specific to sea-age and region, simpler nested models without time trend, or with identical time trend for each region and/or sea-age were considered. Competing models were compared using the Akaike Information Criterion (AIC; Burnham & Anderson, 2002). The reduction of the model deviance as the models get

more parameters (i.e. increase in complexity) was also used to comment on the relative importance of the covariates in explaining the data variability. No data transformation was needed as the residuals from the models did not reveal any departure from the assumptions of normality and homogeneity of variance.

Common fluctuations among regions

Time trends in each life history trait were then examined to test for common temporal fluctuations among regions (for any sea-age strategy). To ensure that two regions would not appear to be correlated simply because both showed comparable long-term trends, any long term trend (low frequency) in the data was first removed by fitting a spline a priori forced to be very smoothed by fixing the degree of freedom to 5 in the GAM procedure. Correlations across years between any two regions were then analysed on the de-trended time series by calculating the Pearson correlation coefficient. Following the methodology developed in Pyper and Peterman (1998), the significance of the correlation was tested using modified Student t-tests with a reduced degree of freedom to correct for any remaining autocorrelation in the de-trended time series.

Comparing rates of change between strategies

We investigated the relative rate of change in life history traits (L, W and K) over the study period to test for potential difference in the intensity of the response between strategies (1SW or 2SW). The average rate of change (in % per year) of each life history trait was directly estimated as the slope of a linear model over time, based on standardized data. The effects of the sea-age and region on the rate of change were introduced as categorical effects, and the year was considered as a continuous variable. Nested models without time trend or with time trends identical for each region and/or sea-age (additive models) were also considered. The best models were selected using the Akaike Information Criterion (AIC; Burnham & Anderson, 2002). Then for each region, the difference in the rate of change (i.e. slope) in the 1SW and 2SW strategies were tested using the Wald test using the '*glht*' function of the '*multcomp*' R package that automatically corrects for multiple comparison.

RESULTS

Differences in mean life history traits between regions and sea-ages

For each trait (L, W, K and D), the data was best explained by a GAM including both an average term and a smoothed temporal trend specific to each combination of region and sea-age (Table II). The average interaction term (region by sea-age) explained most of the observed variability in the data, revealing high differences in the average level of life history traits across sea-age classes and regions. The strongest difference occurred between the North West (Normandy and Brittany) and the South West (Aquitaine) regions. Fish from Aquitaine were noticeably larger and heavier than fish from Normandy and Brittany for both 1SW and 2SW fish. 1SW fish from Normandy were also heavier than in Brittany, but no clear difference was detected in 2SW fish between the two regions. 2SW fish from Aquitaine were caught later than fish from Normandy and Brittany, the average difference in the date of river entry between the three regions being much weaker for 1SW. Comparatively, the smoothed time trends explained a much lower part of the deviance, even when considering an interaction with sea-age and/or region (Table II).

Time trends in life history traits and common fluctuations between regions

Overall, the nonlinear smoothed temporal trends on the 1987-2013 period revealed a general delay in the date of river entry and a decrease in fish weight and length (Figure 2). However,

time trend were specific for each region and sea-age. In particular, the coefficient of condition of fish was more contrasted between sea ages than the other life history traits. K exhibited a clear downward trend in 1SW fish but remained rather stable in 2SW fish. Changes in the date of capture also exhibited differences between regions and sea age. 1SW fish from Normandy and Brittany showed the most important delays of return migration, with a lag of up to 40 days throughout the study period. Meanwhile, the observed delays for 2SW fish and 1SW fish in Aquitaine were only 20 days. Besides, smoothed time trends also suggested synchronous fluctuations across regions with a 7-8 years period, with high similarity between Brittany and Normandy (Figure 2). Variations in size and weight suggested a common temporal pattern across regions, characterized by repeated declines in both phenotypic traits around years 1990, 1998 and 2007.

The analysis of correlations between de-trended time series further support the hypothesis of a synchronous change in L, W, K or D across regions (Table III). Indeed, for each trait, most of the correlations between regions were positive and significant, even after accounting for autocorrelation. The strongest correlations between regions were found for L and W. The strongest correlations were also found between Brittany and Normandy, which are geographically close. Correlations between more distant regions (i.e. Brittany and Aquitaine, Normandy and Aquitaine) were generally weaker. Also, with the exception of D, between-region correlations seemed stronger in 2SW fish than in 1SW fish.

In general, the date of river entry showed opposite trends to length and weight, a later date of river entry being associated with a decline in the length and weight of fish. Interestingly, those

opposite smoothed time trends were also associated with negative correlations at a shorter time scale, with 7-8 years periodicity in the date of river entry being in antiphase with those of length and weight (Figure 2).

Rate of change over the study period (1987-2013)

Consistently with the analyses of non-linear trends, average rates of change in traits were almost all negative (Figure 3) and depended upon both region and sea-age (based on AIC and explained deviance, not shown). Overall, pairwise comparison tests of the difference between rate of change in traits (per sea-age and per region) revealed a stronger decline in W, L and K for 1SW fish than for 2SW fish. The largest rates of change were found for weight, with an average rate of -1.00% per year for 1SW fish and -0.32% per year for 2SW in Brittany. The body condition of 1SW fish declined by 0.20 % (Aquitaine) to 0.51 % (Normandy) per year while the rate of change in K was close to zero for 2SW and could even be positive in some regions. The relative rate of change in L was not different in 1SW and 2SW (p-value > 0.05), fish having lost on average 0.10% (Brittany) to 0.20% (Aquitaine) of their initial body length per year between 1987 and 2013.

DISCUSSION

Our analysis provides new insights on temporal changes in *S. salar* life history traits across France over the last three decades, and contributes to reduce the gap in knowledge by providing further empirical evidence of a long suspected change in life history of *S. salar* throughout its entire distribution area. Using a large dataset from rod and line and commercial catches, we describe a decline in individual length, weight, together with a delay in the migration phenology of adult *S. salar* returning to French rivers. Our analysis highlighted similarities in time trends between regions, but the rate of change in life history traits clearly depends upon the tactic at sea.

Strength and limitation of the data

Time trends in *S. salar* life history traits were analyzed using catch data from recreational and commercial salmonid fishery. This unique dataset provides a large scale observatory of wild French *S. salar* populations. Commercial fisheries of *S. salar* are almost all closed since the early 1990's (ICES, 2016), and scientific data are only available for a few rivers and generally cover only short periods of time. By contrast, recreational hook and line fishery are operating in almost all rivers across the species distribution range. Thus, when available catch data provides to date the broadest spatio-temporal sampling of *S. salar* populations across several countries (Bacon *et al.*, 2009; Valiente *et al.*, 2011; Fjørtoft *et al.*, 2014).

The advantages offered by the large spatial and temporal coverage of this fishery dataset are balanced by the difficulty to control the sampling effort. Recreational fishery data might

indeed suffer from non-random sampling caused by fishery management rules and intrinsic variability in fishing effort (Bacon *et al.*, 2009). Although catch data virtually come from newly arrived fresh-run fish only (Thorley et al., 2005; Bacon et al., 2009), the date of capture may still provide a biased estimate of the date of river entry, and this bias may differ between regions. For instance, fish from Aquitaine generally undertake a longer journey in freshwater before being caught (longer rivers) than fish from Brittany and Normandy (smaller and shorter rivers). Hence, the late migration timing reported for Aquitaine (2SW) may be partly explained by a specific spatial setting compared to the other regions rather than by a latter return to coastal waters. This late migration can also reflect a distinct flow regime in early spring, that is driven by melting snow on the Adour - Gaves rivers (where most catches come from). By contrast, we assume that our results on the relative variability and the rate of change in this trait within a given region are robust.

By removing catches made in the end of fishing season, our analysis might miss key ecological signal. In particular, we would not be able to detect any potential compensatory mechanism that would occur between early and late migrating fish. For instance one can hypothesize that a decline in body size among studied fish might be balanced by an increasing number of large fish in a potential late run. Although we cannot rule out such a process, the late captures represented only a small proportion of fish in France, which may thus have a limited impact on our results. Migration monitoring using a fish trap on the Scorff River shows that less than 10% of all 1SW and 2SW fish were trapped in fall, with no evidence of growth compensation (E. Prévost, pers. com.).

Lastly, although raw data were available at the scale of single rivers, samples were pooled at the regional scale to dampen the effect of uncontrolled sampling variability and local heterogeneity. Indeed, the low signal-to-noise ratio due to low sample size or uncontrolled variation of the fishing effort in space and time for single rivers (e.g., due to alleged report of the fishing effort from one river to the other within the fishing season) would impede the detection of time trends. Aggregating data on several rivers of the same region helped disentangling the temporal variation attributable to large scale environmental change, from local factors.

Evidence for change in phenotypic traits

In France, differences in average phenotypic traits and migration date were detected between regions. Interestingly, those patterns have already been described in previous analyses on older data (Prévost, 1987), thus highlighting the stability of the regional contrast over several decades. As discussed previously, the date of river entry may be overestimated in Aquitaine due to uneven sampling design across regions. Genetic drivers of the migration timing may also be considered (Hansen & Jonsson 1991). But this effect is unlikely to explain weight and length differences. Such phenotypic differences are likely to reflect distinct genetic pools (Perrier at al., 2011).

Overall, this study highlighted important change in phenotypic traits in French *S. salar* populations over the period 1987-2013. In all regions, we detected a significant decline in fish

length and weight, as well as a delay in the date of river entry. Results are consistent with patterns already reported in several other rivers in Northern Europe. Similar declines in *S. salar* length (about 1 cm per decade), weight (200-400 g per decade) or 1SW body condition have been observed in Scotland (Bacon *et al.*, 2009; Todd *et al.*, 2011), Ireland (Quinn *et al.*, 2006), Norway (Jonsson *et al.*, 2016) or North America (Friedland *et al.*, 2005). The observed delay in migration timing (about 5-10 days per decade) is also congruent with previous findings in Scotland (Youngson *et al.*, 2002; Todd *et al.*, 2012), England (Aprahamian *et al.*, 2008) or Spain (Valiente *et al.*, 2011).

Moreover, our correlation analysis highlighted common inter-annual fluctuations in phenotypic traits across all three French regions. Interestingly, we detected more similarities in the temporal variability of those traits between neighboring French Northern regions (Brittany and Normandy) than between these two Northern regions and the more distant Aquitaine. These results support the hypothesis of a segregation of populations by distance (Jensen *et al.*, 2011; Juanes *et al.*, 2004; Perrier *et al.*, 2011), which may be driven by spatial or temporal segregation in post-smolt migration route and feeding zone at sea (Bacon *et al.*, 2009; Jensen *et al.*, 2011) or to a difference in river profiles (Juanes *et al.*, 2004; Valiente *et al.*, 2011). French *S. salar* populations face environmental conditions that differ in many ways from the conditions encountered by Northern Europe populations (e.g. longer migration routes, higher freshwater temperature, high anthropic pressure …). However, the impact of a large scale phenomenon in the marine environment, initially described in Northern Europe, seemed to prevail in France as well. Therefore, by providing empirical evidence for Southern populations, our study nicely complements existing literature to better describe the "big picture".

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452 A response to marine environmental change

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455 Taken together, results suggest a globally coherent response across French populations and
456 beyond, in Northern Europe. They strongly support the hypothesis of a common
457 environmental mechanism affecting *S. salar* population throughout its distribution area.
458 Temporal similarities across regional patterns, e.g. time series varying in phase or antiphase,
459 strongly suggest a response to common environmental drivers jointly impacting the marine
460 phase of the life cycle of different populations spawning in distant rivers. Several studies
461 suggested that a major decline in growth condition would be responsible for the decrease in *S.*
462 *salar* length and weight (Friedland *et al.*, 2000; Peyronnet *et al.*, 2007; McCarthy *et al.*, 2008;
463 Jensen *et al.*, 2011), while within river migration timing increased. As a mechanism, it has
464 been suggested that bottom-up control on food resources during the early marine phase of
465 post-smolts may have negatively impacted both growth and survival (Friedland *et al.*, 2009;
466 Jensen *et al.*, 2011; Beaugrand & Reid, 2012). Triggered by ocean warming, a major trophic
467 shift in the North Atlantic Ocean has been documented in the 1990s, with reported changes in
468 zooplankton communities up to seabird population dynamics (Durant *et al.*, 2004; Beaugrand
469 *et al.*, 2008). As a result, decrease in prey abondance and energetic quality may have altered
470 *S. salar* growth potential at sea (Otero *et al.*, 2012, Mills *et al.*, 2013). Jonsson *et al.* (2016)
471 further noted that direct effect of temperature are unlikely to explain observed changes but
472 argued in favor of an impact of stock rebuilding in the Herring *Clupea harengus* L. 1758, or
473 in other Clupeides species, which may compete for resources with salmon smolt, as observed
474 in the Baltic Sea.

It has been demonstrated that the mortality of fish at sea is size dependent (Lorenzen, 1996; Gislason *et al.*, 2010). In particular, *S. salar* marine mortality is believed to be mostly caused by predation and will then be size- and growth-dependent (Friedland *et al.*, 1993; Friedland *et al.*, 2000), i.e. larger and more robust fish have a higher probability to escape predation. As a consequence, decreasing growth rate at sea may also be responsible for a decline in marine survival, as also suggested by synchronous patterns across Northern Europe reported by several authors (Friedland *et al.*, 1993; Friedland *et al.*, 2000; Peyronnet *et al.*, 2007; Chaput 2012). However, our catch data do not inform about survival in French populations. Nevertheless, *S. salar* monitoring using a fish trap on the Scorff river showed substantial change in marine survival, the average return rate decreasing from 10,3 % (1997-2003) in the 2000's to 4,8 % in recent years (2009-2013) (ICES, 2016).

The temporal coherence (i.e. direct anti-phase) in declining length/weight and delaying run migration observed in our populations appeared compatible with such a degradation of feeding conditions at sea. Within a given sea-age class, the spawning run lasts several weeks, and its seasonal timing is expected to be driven by the tradeoff between reproduction and survival. The reproductive benefit associated with extra feeding opportunities at sea would be balanced against the risk of mortality during an extra time at sea (Clark, 1994). As a consequence, decreasing growth rate may call for an extra time at sea, aiming at maximizing growth potential, as observed in some Scottish rivers (Todd *et al.*, 2012). However, if resource conditions turn out to be so degraded, the decline in growth rate would be too large to be compensated by a mere delay in the date of river entry. Such a mechanism may generate

opposite patterns of temporal variability in migration timing and length or weight (using de-trended data), as observed in French populations. Interestingly, Valiente *et al.* (2011) also reported negative correlations between medium term fluctuations of length/ weight and the date of river entry.

Different responses between 1SW and 2SW

Our results stressed that the relative change in weight and condition of returning *S. salar* was weaker and less variable in 2SW than in 1SW. Similar differences between 1SW and 2SW seemed to be present in Scottish (Bacon *et al.*, 2009) and Norwegian populations (Jonsson & Jonsson, 2004) as well. Thus, there is a need to better account for differences in *S. salar* anadromous tactics to better understand the demographic and ecological mechanisms underlining population changes.

1SW and 2SW *S. salar* have first similar migration routes at the beginning of their journey at sea and then separated migration routes where they may encounter different growth condition at sea. One cannot exclude that change in the feeding condition experienced by 1SW has been more stringent than in 2SW fish, thus explaining a weaker decline in 2SW weight. A proportionally lower decrease in the length of 2SW fish may also point at some compensatory mechanism. For instance, 2SW may move toward more favorable feeding grounds which would then support a higher growth rate over the second year at sea (Auer *et al.*, 2010; Hogan & Friedland, 2010). However, this hypothesis appears poorly supported by recent studies that

analyzed growth patterns on fish scales for Northern populations, showing that growth increment in 2SW during the second year at sea was not significantly higher than growth rate over their first year at sea (Hogan & Friedland, 2010; Jensen *et al.*, 2011; Jonsson *et al.*, 2016).

In *S. salar*, the duration of the marine phase of the life cycle may reflect different strategy of resource allocation between key fitness components (e.g. survival, growth, reproduction). Intrinsic difference in allocation rule may generate contrasted response to a given change in resource availability between 1SW and 2SW fish. Females are largely dominant among 2SW fish (Baglinière & Porcher, 1994; Fleming, 1996; Barson et al. 2015), thus suggesting that difference in allocation rule between 1SW and 2SW could emerges from difference in allocation rules between males and females. Noteworthy, males and females have specific physiological and behavioral constraints over the reproduction period; they are also characterized by distinct tactics at sea. In *S. salar*, female's fitness is more strongly driven by body size than male's one because sexual maturation process requires greater energetic needs in females than in males (i.e. to maximize fecundity). The tight dependence between sex and sea age classes might explain the difference in individual's response to changes in environmental conditions between sea ages classes. As a result, 1SW fish (preferentially males) might have favored activities related to survival at the expense of mass gain, and 2SW fish (preferentially females) might have favored a large body size as a way to maximize fecundity in surviving individuals, as suggested by our data.

In more details, the rate of change was not uniform for all life history traits in 1SW and 2SW. Actually, we highlighted a similar response in 1SW and 2SW across regions for body length. In *S. salar*, growth and body size are considered as key drivers of marine survival and female fecundity (Thorpe *et al.*, 1984; Fleming, 1996; Jonsson *et al.*, 1996). But a large body size is also a key feature of reproduction success in anadromous males, as it confers an advantage in terms of intra-sexual competition for mate (Fleming, 1996). Therefore fish length appears as an important fitness component (Marschall *et al.*, 1998) in both males and females, i.e. in both 1SW and 2SW fish. Not surprisingly, length happened to be the most preserved life history trait in our analysis: low variability and weak decline. Similarly Todd at al. (2008) reported a disproportional decline in body weight compared with length in Scottish 1SW fish (22% vs. 4% declines, respectively). This pattern seems consistent with the life history theory, which states that phenotypic traits the more strongly connected to fitness are expected to be the more preserved - or canalized - against environmental stochasticity (Stearns & Kawecki, 1994; Pfister, 1998; Caswell, 2001; Gaillard & Yoccoz, 2003). At the population level, the relative conservatism in body length, compared to other traits, can be perceived as a positive signal for population viability.

Conclusion

This large scale study on French populations contributes to reduce the gap in knowledge by providing further empirical evidence of a long suspected change in life history of *S. salar* throughout its North East distribution area. Results also revealed different rates of change between 1SW and 2SW fish, thus pointing out the importance of considering the complexity

of life history strategies when exploring mechanisms of changes in *S. salar* phenotypic traits. We hope that this long due analysis for France would encourage other authors to make their dataset available to the scientific community, which is a prerequisite to improve our understanding of major cross-border ecological mechanisms.

Acknowledgments

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815 Tables

816 Table I. Sample size: number of 1SW and 2SW *S. salar* per region considered in the study.

Age	Normandy	Brittany	Aquitaine
1SW	3716	12053	959
2SW	3110	9577	3870

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818

819 Table II. Modelling date of river entry, length, weight and condition in *S. salar* caught in
820 France as a function of sea age (A), region (R) or year (Y). Deviance explained, F-test p-
821 values and delta AIC are presented for each model. s() indicated GAM smoothing.
822

	Date of river entry		Length		Weight		Condition	
Covariates	Dev exp	ΔAIC	Dev exp	ΔAIC	Dev exp	ΔAIC	Dev exp	ΔAIC
A×R	61.26	-91970	71.94	-153634	68.68	-91117	3.34	-11314
A×R+s(Y)	63.7	-1790	72.84	-889	70.17	-1335	5.24	-533
A×R + s(Y,by=A)	64.47	-572	72.95	-95	70.29	-96	6.26	-283
A×R+s(Y,by=A×R)	64.95	-313	73.17	-161	70.55	-177	6.65	-61

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825 Table III. Cross-correlations in date of river entry, length, weight and condition between
826 regions for each sea-age class. The significance of the tests is presented as follow: "***",
827 "**", "*" and "." correspond to p-values inferior or equal to 0.001, 0.01, 0.05 and 0.1,
828 respectively. The p-values are corrected to account for the autocorrelation in the times series.
829

	Normandy / Brittany	Normandy / Aquitaine	Brittany / Aquitaine
1SW Date	0.46*	0.38*	0.01
1SW Length	0.35.	0.56**	0.57**
1SW Weight	0.46*	0.44*	0.68***
1SW Condition	0.47*	0.34.	0.45*
2SW Date	0.32.	0.01	-0.02
2SW Length	0.75***	0.54**	0.52**
2SW Weight	0.86***	0.57**	0.42*
2SW Condition	0.66***	0.46*	0.25

830
831

832 Figure captions

833 Figure 1. Description of the three regions considered in the analysis: Normandy, Brittany and
834 Aquitaine. In each region, the name of the rivers that provided *S. salar* captures are presented.

835

836 Figure 2. Change in the date of river entry, length, weight and condition in 1SW and 2SW *S.*
837 *salar* from Normandy, Brittany and Aquitaine.

838

839 Figure 3. Linear rate of change in the date of river entry (D), length (L), weight (W) and
840 condition (K) in 1SW and 2SW *S. salar* from Normandy (N), Brittany (B) and Aquitaine (A).
841 The the difference in the rates of change between 1SW and 2SW was assessed with a Wald
842 test. The significance of the test is presented as follow: "***", "**", "*" and "." correspond to
843 p-values inferior or equal to 0.001, 0.01, 0.05 and 0.1, respectively.

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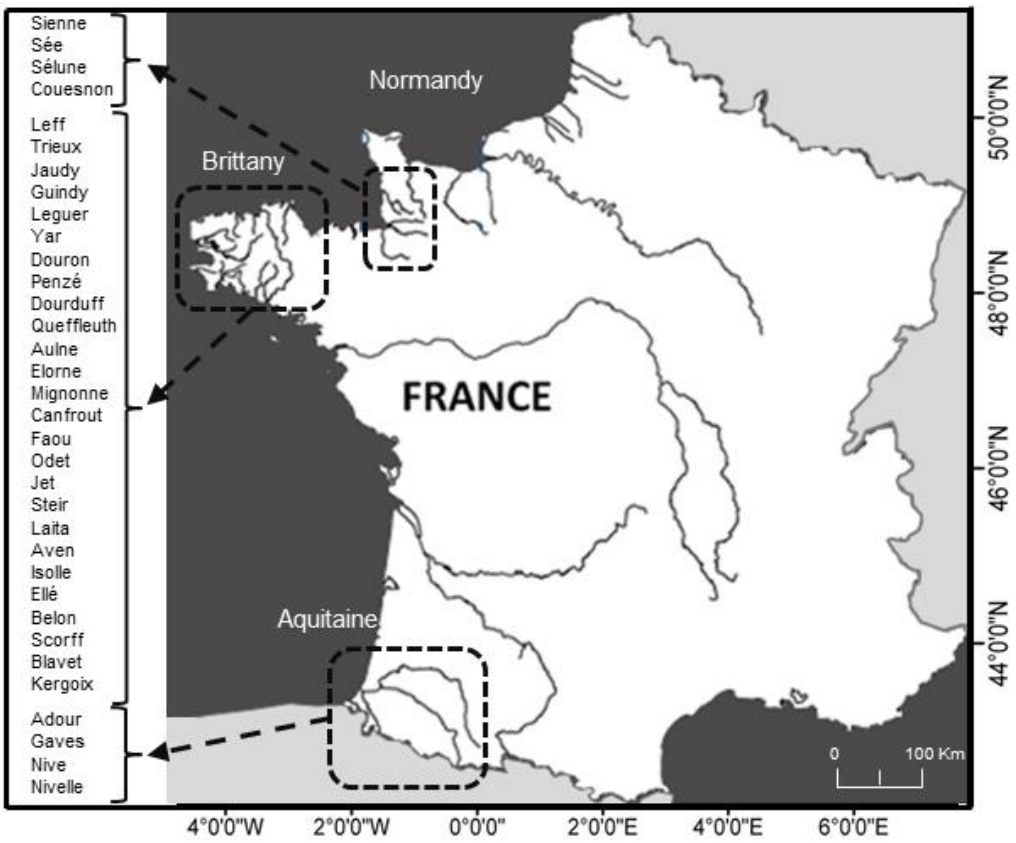
845

846 Figure 1



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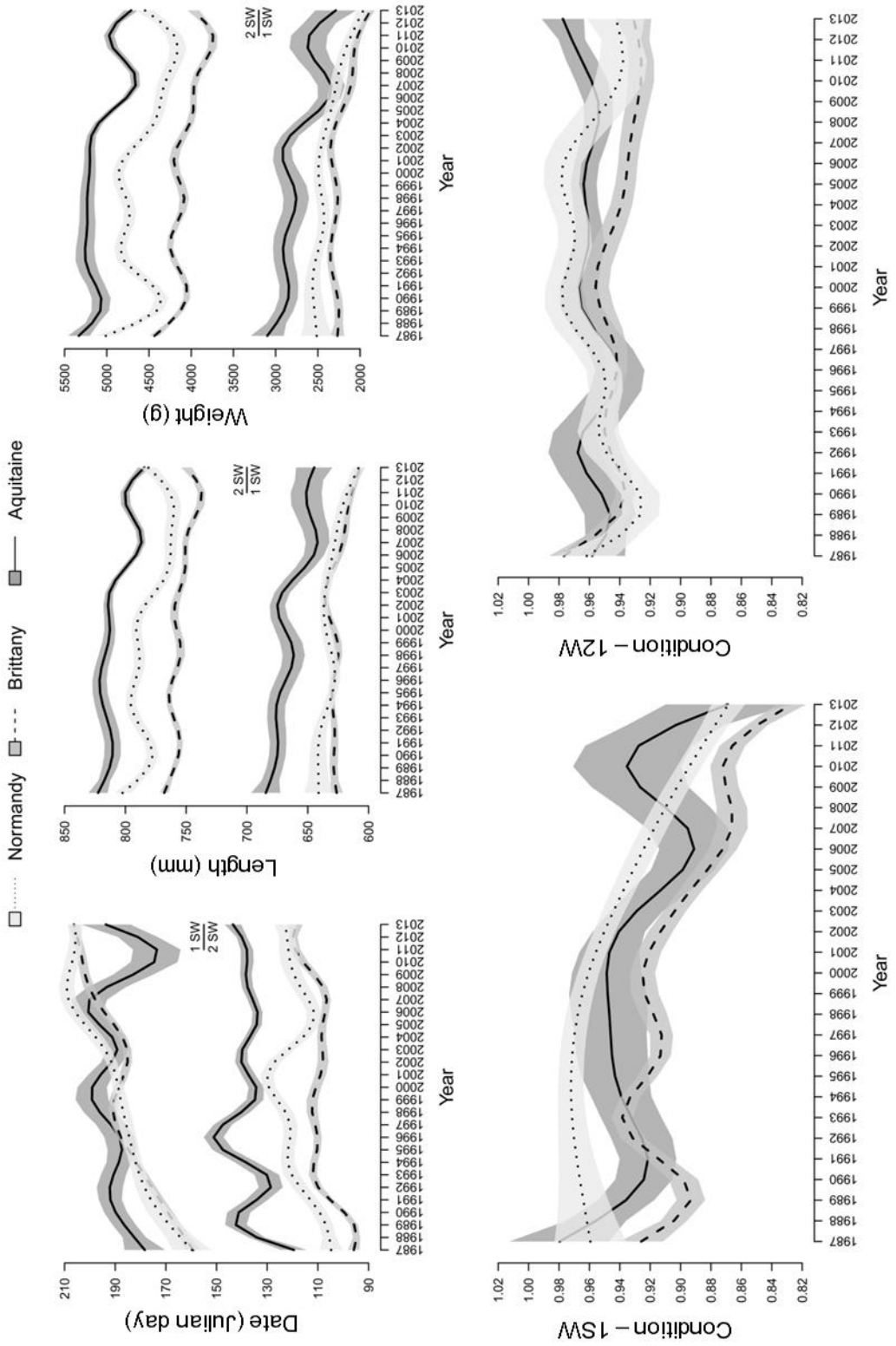
849 Figure 2



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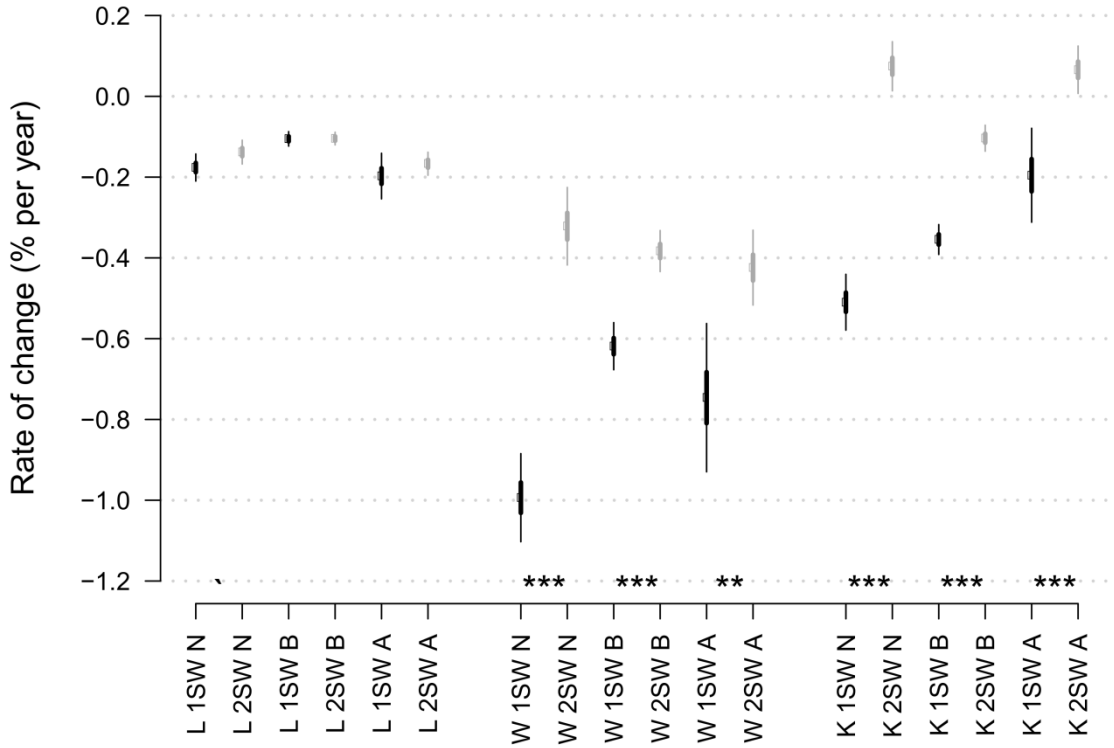
853 Figure 3



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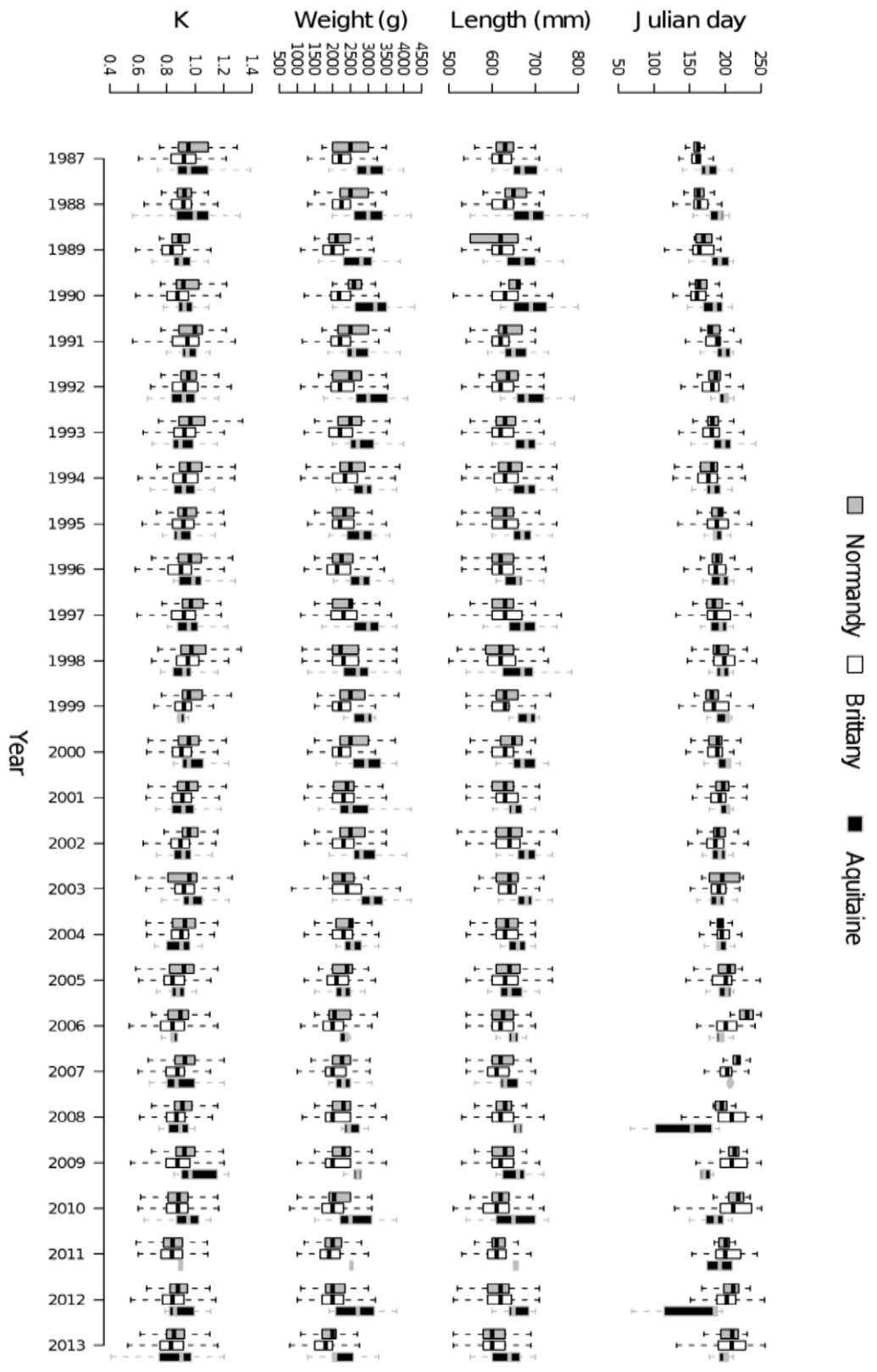
Supporting information

Figure captions

Figure A1. Boxplots of raw data for the date of river entry, the length, the weight and the condition (K) of 1SW fish caught by the French hook and line recreational salmon fishery (spring and summer catches).

Figure A2. Boxplots of raw data for the date of river entry, the length, the weight and the condition (K) of 2SW fish caught by the French hook and line recreational salmon fishery (spring and summer catches).



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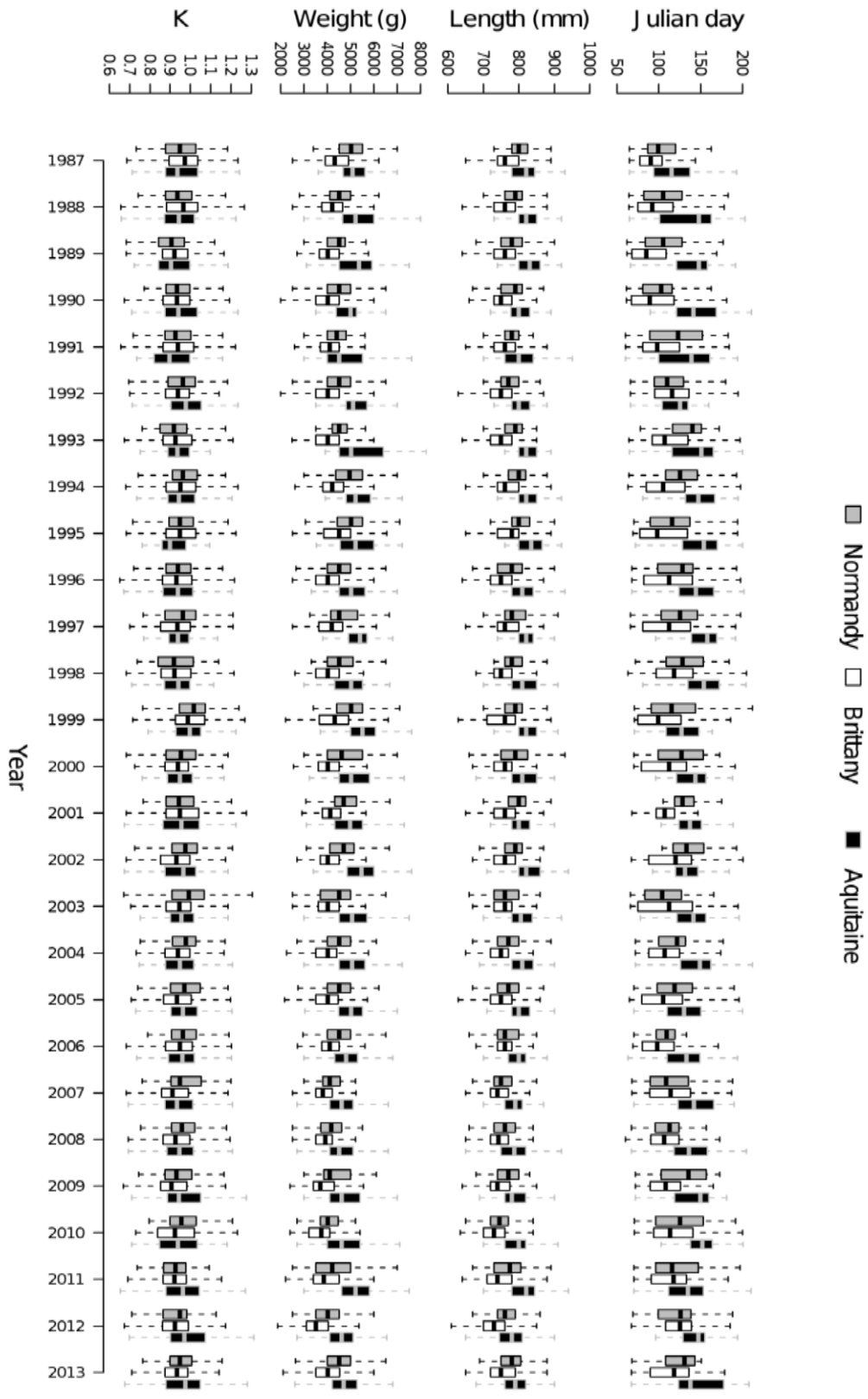
868 Figure A1.



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870 Figure A2.